# Response of tree roots to decomposing organic matter in two lowland Amazonian rain forests

T. V. St. John

*Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO, U.S.A. 80523*

Received August 23, 1982[1]

Accepted November 15, 1982

St. John, T. V. 1983. Response of tree roots to decomposing organic matter in two lowland Amazonian rain forests. Can. J. For. Res. **13**: 346–349.

Fine roots of tropical rain forests are sometimes associated with decomposing organic matter at the soil surface. This association is considered by some authors to be important in recovery of nutrients by the vegetation. In this paper, experimental evidence is presented to show that the association results from a dynamic process and is not a coincidental result of negative geotropism. The association appears to be the result of random encounters of growing roots with organic matter, followed by

[1]Revised manuscript received November 9, 1982.

increased branching at that site. The concentration of absorbing tissue in such relatively nutrient-rich sites as decomposing organic matter implies more effective ion absorbtion than would result if roots were randomly distributed in the soil volume.

ST. JOHN, T. V. 1983. Response of tree roots to decomposing organic matter in two lowland Amazonian rain forests. Can. J. For. Res. **13**: 346–349.

Les radicelles dans les forêts ombrophiles tropicales sont quelquefois associées à la matière organique en décomposition à la surface du sol. Certains auteurs estiment que cette association est importante dans la récupération des éléments par la végétation. À partir d'une évidence expérimentale, on montre ici que l'association en question est le résultat d'un processus dynamique et qu'elle n'est pas une coïncidence attribuable à du géotropisme négatif. L'association semble être le résultat de rencontres au hasard de racines en croissance avec de la matière organique suivies d'une augmentation des ramifications au lieu de la rencontre. La concentration des tissus absorbants dans des lieux relativement riches en éléments nutritifs comme la matière organique en décomposition se traduit par une absorption plus efficace des ions que si les racines étaient distribuées au hasard dans le sol.

[Traduit par le journal]

## Introduction

An association of forest roots with decomposing organic matter (OM) has been noted in several forest ecosystems (Damman 1971; Kimmins and Hawkes 1978; Woods 1957). In certain Amazonian rain forests most of the fine-root biomass lies above the mineral soil in a layer of humus and detritus (Klinge 1973; Klinge and Herrera 1978; Stark and Spratt 1977). Observations of this root mat led Went and Stark (1968), in their well-known direct nutrient cycling theory, to suggest that the association of fine roots and OM causes efficient recovery of nutrients in the tropical rain forest. Jordan and Herrera (1981) and Jordan (1982) also considered this a specific adaptation for nutrient recovery in the Amazon.

The following alternative hypotheses could account for the root–OM association. (*i*) Roots come to the surface because of negative geotropism (Lyford 1975). (*ii*) Aluminum toxicity (Foy 1974), flooded soil, or another inhibitory factor in mineral soil means the roots are able to grow only at the surface. (*iii*) Roots display some sort of tropism for nutrients (Liebig, quoted by Weaver 1926) or organic matter (Stark 1971). (*iv*) Roots grow in an unbranched extension mode until randomly encountering organic matter, then convert to a highly branched mode (Lyr and Hoffman 1967; Rogers and Head 1969), with the result that the greatest proportion of fine roots appears in association with organic matter. The first two hypotheses imply that the root–OM association is only coincidental. Hypotheses (*i*) and (*iii*) were examined experimentally and hypotheses (*ii*) and (*iv*) were examined deductively, based on characteristics of the site and analysis of the experimental results.

## Methods

*Study sites*

The experiments were carried out at two sites in old-growth lowland evergreen rain forests near Manaus, Brazil. The sites were chosen because they differed greatly in amount of aboveground root growth, in species composition of the forest, and in soil properties. Sites 1 and 2, both on non-flooded soil, were on Oxisol and Entisol (white sand), respectively. At both sites annual precipitation was about 2000 mm, with a drier period from July to September. Experiments at both sites were carried out entirely during the wet season. Site 1, described by Prance *et al.* (1976), had little accumulated surface litter. Where a litter layer was found, fine roots usually grew into it from underlying soil. At site 2, described by Anderson *et al.* (1975), humus and litter occurred on the soil surface over most of the site, and ranged from 4 to 10 cm in depth. Most of the fine roots of the forest were associated with this layer.

The method for determining the response of roots to the decomposing leaves was adapted from Lund *et al.* (1970). Plastic mesh bags were filled with 2 kg of sand (control) or 1 kg of sand and an equivalent volume of decomposing leaf litter of *Theobroma cacao* L. The litter, collected in a plantation near site 1, was a mixture of material varying in age from zero to a few weeks. All material consisted of easily recognizable cacao leaves in early stages of decomposition. The bags were about 40 cm in length, 10 cm in width, with mesh openings of about 5 mm. These dimensions are approximate because width and mesh size varied with distension of the material.

The bags were inserted into holes made with a 10-cm-diameter soil-sampling tube. Any organic layer was lifted away, and a hole was made to a depth of approximately 20 cm. Each mesh bag was enclosed in an inverted plastic bag, folded to retain the bag's contents until it was in place. The plastic bag was then withdrawn. The necks of the yellow mesh bags were left exposed on the soil surface to aid in sample recovery. The organic layer, when present, was pressed back into place around the bags. Fifteen bags of each treatment were placed at each site, interspersed throughout a rectangular area of about 20 × 30 m. The bags were left in place for 30 days. At harvest they were withdrawn, severing the roots where they entered the bag. The total length of root in each bag, which included roots that entered from surrounding soil and any branches these produced in the bag, was determined by the method of Newman (1966).

## Results

In some treatments fewer than 15 bags were recovered. Root lengths were much greater in OM treatments

TABLE 1. Root growth experiments in two tropical terra firme forests near Manaus, Brazil

| | Control | OM |
|---|---|---|
| Site 1 | | |
| Mean root lengths (CM) ± SE | 9.28±2.36 | 135±44.9 |
| No. of observations | 14 | 13 |
| Site 2 | | |
| Mean root lengths (CM) ± SE | 14.3±3.70 | 125±45.8 |
| No. of observations | 15 | 15 |

TABLE 2. The number of bags with no roots in control and organic matter treatments, two forest sites combined; $p$ of this or a more extreme table = 0.226, NS, by Fisher's exact probability test (Siegel 1956)

| | Control | Organic matter |
|---|---|---|
| No roots | 5 | 2 |
| Roots present | 24 | 26 |

at both sites (Table 1). Owing to the skewed distribution of values the Wilcoxon rank sum test (large-sample approximation; Hollander and Wolfe 1973) was applied. At both sites the root lengths were significantly greater in the OM treatment than in the control (Table 1; $W^* = 2.80$, $p < 0.01$, and $W^* = 2.20$, $p < 0.05$, respectively).

The proportion of bags in which no roots had appeared was analyzed by combining data from the two sites (Table 2). The Wilcoxon rank sum test applied separately showed the corresponding treatments to be statistically indistinguishable. It was shown by Fisher's exact probability test (Siegel 1956) that the proportions of bags lacking roots could occur by chance 23% of the time. This indicates that roots were no more likely to enter an organic matter bag than a control bag.

## Discussion

The experiment showed a specific response of root length to decomposing OM. The results and conditions of the experiment may be used to distinguish between the alternative hypotheses suggested in the introduction. Negative geotropism is ruled out because both control and OM treatments were at equal depths in the soil. Flooding cannot be implicated because at both sites the water table is below the soil surface during the entire year and in any case would have affected control and OM treatments similarly. Aluminum content was about 2.81 mequiv./100 g of mineral soil at site 1 and about 1.15 mequiv./100 g at site 2 (Anonymous 1969), but root development in the organic horizon was greater at site 2. Aluminum toxicity was more severe at the field site with less surface root development and thus is not the main factor controlling root distribution. Aluminum was not determined in the two experimental treatments, but should have been similar or higher in the presence of decomposing OM. Tropism for organic matter is eliminated because the proportions of zero root lengths, reflecting the probability that outside roots will not enter the bags, were not significantly different. The remaining possibility, that extending roots encountered the OM-enriched bags at random, then branched more profusely at those sites, is consistent with the observations and explains the increased root length in the OM treatment. The branching response of these roots is consistent with the finding that organic matter with an active microflora led to increased root branching in laboratory conditions (St. John and Machado 1978).

TABLE 3. Frequency distribution of length of roots in organic matter treatment, two sites combined. Class limits are from 0.49 below to 0.5 m above the integer value (zero class includes 0–0.5 m)

| Root length (m) in classes | No. bags in class |
|---|---|
| 0 | 12 |
| 1 | 9 |
| 2 | 1 |
| 3 | 3 |
| 4 | 1 |
| 5 | 1 |
| 6 | 1 |

NOTE: $U = 0.043 \pm 0.3$ (this frequency distribution is satisfactorily described by the negative binomial (Bliss and Fisher 1953)).

A random process (encounter of roots with organic matter) followed by a growth process (branching in each bag) should lead to a contagious frequency distribution, indicating "aggregation." The root lengths in combined OM treatments, divided into classes, fit the negative binomial distribution (Table 3) by the $U$-test (Bliss and Fisher 1953). The negative binomial is an example of a frequency distribution that often satisfactorily describes aggregated organisms in nature.

The association between fine roots and decomposing OM means that the plant is essentially rooted in a medium richer in nutrients than the bulk soil. Diffusion often limits uptake of nutrients in soil, and additional roots in a locally rich site led to increased uptake in many circumstances (Barley 1970). Thus in at least these two tropical forests, there is a specific mechanism by which fine absorbing roots place themselves at the site of most nutrient mineralization and in so doing probably lead to improved mineral recovery and decreased mineral loss from the ecosystem.

## Acknowledgments

I thank Drs. J. D. Lebreton, J. S. Singh, D. C.

Coleman, C. P. P. Reid, J. A. Trofymow, K. A. Vogt, and H. W. Hunt for discussions and for critically reading an earlier version of the manuscript. Portions of this work were supported by a grant from the Brazilian National Research Council to Dr. Paulo de Tarso Alvim and preparation of the manuscript by National Science Foundation grants DEB 78-11201 and 80-04193.

ANDERSON, A. B., G. T. PRANCE, and B. W. P. DE ALBUQUERQUE. 1975. Estudos sobre a vegetação das campinas Amazonicas. III. A vegetação lenhosa da campina da reserva biológica INPA-Suframa (Manaus-Caracarai, km 62). Acta Amazonica, **5**: 225–246.

ANONYMOUS. 1969. Os solos da area Manaus-Itacoatiara. Studies and tests series No. 1, Public Relations Sector, Instituto de Pesquisas e Experimentaçao Agropecuarias do Norte, Belem, Brazil.

BARLEY, K. P. 1970. The configuration of the root system in relation to nutrient uptake. Adv. Agron. **22**: 159–201.

BLISS, C. I., and R. A. FISHER. 1953. Fitting the negative binomial distribution to biological data, and a note on the efficient fitting of the negative binomial. Biometrics, **9**: 176–200.

DAMMAN, A. W. H. 1971. Effect of vegetation changes on the fertility of a Newfoundland forest site. Ecol. Monogr. **41**: 258–268.

FOY, C. D. 1974. Effects of aluminum on plant growth. *In* The plant root and its environment. *Edited by* E. W. Carson. University of Virginia Press, Charlottesville, VA. pp. 601–642.

HOLLANDER, M., and D. A. WOLFE. 1973. Nonparametric statistical methods. John Wiley and Sons, New York.

JORDAN, C. F. 1982. Amazon rain forests. Am. Sci. **70**: 394–401.

JORDAN, C. F., and R. HERRERA. 1981. Tropical rain forests: are nutrients really critical? Am. Nat. **117**: 167–180.

KIMMINS, J. P., and B. C. HAWKES. 1978. Distribution and chemistry of fine roots in a white spruce – subalpine fir stand in British Columbia: implications for management. Can. J. For. Res. **8**: 265–279.

KLINGE, H. 1973. Root mass estimation in lowland tropical rain forests of central Amazonia, Brazil. I. Fine root masses of a pale yellow latosol and a giant humus podzol. Trop. Ecol. **14**: 29–38.

KLINGE, H., and R. HERRERA. 1978. Biomass studies in Amazon caatinga forest in southern Venezuela. I. Standing crop of composite root mass in selected stands. Trop. Ecol. **19**: 93–110.

LUND, Z. F., R. W. PEARSON, and G. A. BUCHANAN. 1970. An implanted soil mass technique to study herbicide effects on root growth. Weed Sci. **18**: 279–281.

LYFORD, W. H. 1975. Rhyzography of non-woody roots of trees in the forest floor. *In* The development and function of roots. *Edited by* J. G. Torrey and D. T. Clarkson. Academic Press, London. pp. 179–196.

LYR, H., and G. HOFFMAN. 1967. Growth rates and growth periodicity of tree roots. Int. Rev. For. Res. **1**: 181–236.

NEWMAN, E. I. 1966. A method of estimating the total root length in a sample. J. Appl. Ecol. **3**: 139–145.

PRANCE, G. T., and W. A. RODRIGUES, and M. F. DA SILVA. 1976. Inventario florestal de um hectare de mata de terra firme km 30 da estrada Manaus-Itacoatiara. Acta Amazonica, **6**: 9–35.

ROGERS, W. S., and G. C. HEAD. 1969. Factors affecting the distribution and growth of roots of perennial woody species. *In* Root growth. *Edited by* W. J. Whittington. Plenum Press, New York. pp. 280–295.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Company, New York.

STARK, N. 1971. Nutrient cycling: I. Nutrient distribution in some Amazonian soils. Trop. Ecol. **12**: 24–50.

STARK, N., and M. SPRATT. 1977. Root biomass and nutrient storage in rain forest oxisols near San Carlos de Rio Negro. Trop. Ecol. **18**: 1–9.

ST. JOHN, T. V., and A. D. MACHADO. 1978. Evidencia da ação de microorganismos na ramificação de raizes. Acta Amazonica, **8**: 9–11.

WEAVER, J. E. 1926. Root development of field crops. McGraw-Hill Book Company, New York.

WENT, F. W., and N. STARK. 1968. Mycorrhiza. BioScience, **18**: 1035–1039.

WOODS, F. W. 1957. Factors limiting root penetration in deep sands of the Southeastern Coastal Plain. Ecology, **38**: 357–359.